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Preface

Nematode-bacterium symbioses: Crossing kingdom and disciplinary boundaries

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Abstract

One of the most common eukaryote-prokaryote interactions is that between nematodes and bacteria. The range of associations between nematodes and bacteria is incredibly broad, ranging from fortuitous to obligate and from beneficial to pathogenic and occurring in all possible habitats. Numerous researchers worldwide are studying associations between these two groups of organisms, but these scientists occupy many different disciplines, and often do not interact. Not surprisingly these researchers come from diverse backgrounds in medicine and veterinary science, entomology, plant biology, genetics etc., yet to date no common coherent ground exists connecting the science being done in *nematode-bacterial interactions* despite the fact that advances in each will undoubtedly inform the others. Furthermore, a comparative approach *between species pairs, or between different research angles* has the power to reveal common underlying themes of nematode-bacterium associations as well as fundamental questions or research topics of symbiosis. For the first time, researchers working on different nematode-bacterium systems were gathered under a unifying theme, a workshop on 'Nematode-Bacterium Symbioses' that was held at the University of Arizona, Tucson, Arizona from April 21 to 23, 2007. The goals of this workshop were threefold: 1) Foster interdisciplinary collaborations among scientists; 2) Break down barriers among researchers studying different taxonomic groups of nematode-microbe associations; and 3) Encourage scientists engaged in basic and applied research to explore how cross-talk and networking can enhance and advance science in this field. Keynote speakers presented on a broad range of taxa and topics pertaining to microbe-nematode interactions, including ecto- and endosymbiosis, beneficial symbioses, multitrophic interactions, pathogenesis, host recognition, colonization processes, genetics and genomics.

Keywords: Symbioses, nematodes, bacteria, model systems, multidisciplinary, workshop

Intimate associations between prokaryotes and eukaryotic hosts are widespread in nature, occurring in every type of ecological niche (Margulis, 1998). The spectrum of such interactions ranges from highly integrated obligatory symbioses to loose associations (Margulis, 1998; Bordenstein, 2003). Symbionts have adapted to their hosts with astounding sophistication, being able, in many cases, to control their *host* reproduction, behavior and overall physiology (Cheng, 1970; Douglas, 1994; Ishikawa, 2003). Understanding how microorganisms and their hosts interact with each other and at different biological levels is of fundamental importance. For example, how symbionts move between host species, how host and symbionts adapt to each other physiologically and genetically, and what evolutionary consequences result from microbial-host associations, are some of the key questions.

Nematodes are one of the most ubiquitous life forms. Numerically they account for up to 80% of all animals, and they occupy all ecological niches (Lamshead et al., 2003). Approximately 50% of known nematode species live in marine habitats, 25% are free-living species found in soil or freshwater, 15% are parasites of animals (vertebrates and invertebrates), and 10% are parasites of plants. In all these habitats and life styles, an assortment of associations exists between nematodes and bacteria ranging from fortuitous to obligatory, and from beneficial to detrimental for the

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nematode hosts. Studies of nematode-bacterium associations have yielded extensive insights in numerous fields of biology, including ecology (e.g., multitrophic interactions, trophic cascades), plant, animal and human pathology, immunology, genetics, genomics, among many others. For example, it has been shown that terrestrial free-living nematodes help distribute bacteria through the soil and along roots by carrying live and dormant microbes on their surfaces and in their digestive systems (Knox et al., 2004).

Furthermore, many nematode species also disseminate or vector pathogenic bacteria. Thus, the ring nematode (*Criconemella* spp.) vectors *Pseudomonas syringae*, the bacterium responsible for the bacterial canker in stone fruit trees, while *Caenorhabditis elegans* carries the human pathogens *Salmonella enterica* and *Escherichia coli* O157:H7 into fruits and vegetables (Kenney et al., 2005). In marine environments, free-living nematodes have ectosymbiotic associations with sulphur-oxidizing chemoautotrophic bacteria that are attached to the nematode cuticle. In this symbiotic association, the nematodes supply the bacteria with oxygen and sulphide (by migrating through the chemocline in sandy sediments), and in turn the bacteria provide carbon as a nutritional source to their nematode hosts (Ott et al., 2002; Polz et al., 1999). Beneficial associations also exist in terrestrial environments, such as between insect-parasitic nematodes and the gram-negative bacteria *Xenorhabdus* and *Photorhabdus* spp. These nematodes and their symbiotic bacteria form an insecticidal complex that is able to kill insects in 24–48 h and is currently exploited as an environmentally safe alternative for control of agriculture and forestry soil insect pests (Akhurst and Boemare, 1990).

Wolbachia bacteria have broad effects on their hosts, ranging from sperm-egg incompatibility to feminization. In the veterinary and human medicine arenas, the discovery of a mutually beneficial association between *Wolbachia* bacteria and filarid nematodes spurred new insights into the pathogenesis and treatment of filariasis (Casiraghi et al., 2001; Lo et al., 2002; Dedeine et al., 2003). It is now recognized that filarial nematodes rely on their *Wolbachia* symbionts for normal reproduction, and that many of the symptoms of filarial diseases (e.g., river blindness and dog heartworm) are caused by the bacterial symbiont rather than the nematode (Taylor, 2000). These discoveries have prompted intense efforts to understand the molecular mechanisms by which *Wolbachia* interacts with its nematode and vertebrate hosts.

Close associations between nematodes and bacteria may even have resulted in DNA exchange between them: evidence suggests that bacterial sequences have been horizontally gene transferred (HGT) into nematode genomes (Bird et al., 2003). Furthermore, Bird and collaborators hypothesized that acquisition of new traits from bacteria (via HGT) has played a central role in speciation of plant-parasitic nematodes, with an intermediate, symbiotic association between nematode and bacteria preceding gene transfer from soil bacteria into proto-parasitic (or even free-living) species.

At present, numerous researchers worldwide are studying associations between these two groups of organisms. The scope of such research is mostly dictated by nematode trophic groups (e.g. plant-parasitic, free living, bacteriovores) or parasitic affiliation (e.g. filarid nematodes and *Wolbachia* associations, insect-pathogenic nematodes and symbiotic bacteria). To date, no common coherent ground exists connecting the science being done in this discipline, despite the fact that advances in each will undoubtedly inform the others. Furthermore, a comparative approach has the power to reveal common underlying research approaches of nematode-bacterium associations as well as fundamental aspects of symbiosis. For example, an integrated view of nematode-bacterium associations will clarify evolutionary questions such as how symbioses impacted nematode speciation and niche expansion. It will permit the identification of common molecular factors mediating nematode-bacterial interactions and the contributions bacteria can make to nematode development. These in turn could reveal novel approaches to help control nematode parasites. The diversity of interactions of nematodes and bacteria, as well as the wealth of knowledge regarding specific interactions, provides an unprecedented opportunity to pursue such a comparative approach.

To address the dearth of communication among scientists studying nematode-bacterium symbioses, a workshop was organized at the University of Arizona from April 21 to 23, 2007, to facilitate the growth and maturation of this topic as a unified discipline. The goals of this workshop were to 1) Foster interdisciplinary collaborations among scientists; 2) Break down barriers among researchers studying different taxonomic groups of nematode-microbe associations; and 3) Encourage scientists engaged in basic and applied research to explore how cross-talk and networking can enhance and advance science in this field.

Four sessions were organized and keynote speakers presented on a broad range of taxa and topics pertaining to nematode-bacterium interactions, including ecto- and endosymbiosis, beneficial symbioses, multitrophic interactions, pathogenesis, host recognition, colonization processes, genetics and genomics.

Keynote presentation titles and speakers are listed below.

Session 1: Free-living nematodes and bacterial symbioses

– Resistance of *Bacillus* spp. to *C. elegans* predation. Jonathan Dworkin, Columbia University.
– Tritrophic interactions of *Pristionchus* nematodes. Ralf Sommer, Max Planck Institute, Germany.

- Ectosymbioses: When bacteria hitch a ride. Martin Polz, Massachusetts Institute of Technology.
- Role of free-living marine nematodes and bacteria in the transformation of organic matter in benthic ecosystems. Valentina Galstova, Zoological Institute, Russian Academy of Sciences.

Session 2: Entomopathogenic nematodes and their symbiotic bacteria

- *Steinernema-Xenorhabdus* complex: Receiving protection and loving companionship. Patricia Stock, University of Arizona.
- Examining the molecular basis of the *Xenorhabdus nematophila-Steinernema carpocapsae* mutualism. Heidi Goodrich-Blair, University of Wisconsin, Madison.
- *Xenorhabdus nematophila* biofilms. Creg Darby, University of California, San Francisco.
- Phoresy among *Paenibacillus* spp. and the entomopathogenic nematodes of Florida citrus orchards. Larry Duncan, University of Florida.
- Predicting niche-specific prokaryotic assemblages using protein domains. Barry Goldman, Monsanto.
- Invasion of the body snatchers: Adhesion, invasion and matricide during *Photorhabdus* transmission by insect parasitic nematodes. Todd Ciche, Michigan State University.

Session 3: Filarid nematodes and bacterial partnerships

- Cysteine proteases and protease inhibitors of filarial nematodes: from genome to biology. Sara Lustigman, Lindsley F. Kimball Research Institute.
- Filaria and *Wolbachia* – a differential role in host immune responses. Katrin Daehnel, Center for Global Health and Diseases, Ohio.
- Genomic analyses of the parasitic nematode *Brugia malayi* and its *Wolbachia* endosymbiont to help map host-parasite interactions. Elodie Ghedin, University of Pittsburgh School of Medicine.

Session 4: Beneficial and pathogenic interactions between plant-parasitic nematodes and bacteria

- Mechanisms and evolution of symbiosis: parasites and mutualists invade plants via a shared response pathway. David Bird, North Carolina State University.
- *Pasteuria* spp., endospore forming bacteria with biological control potential. Donald Dickson, University of Florida.
- Bacterial endosymbionts in plant parasitic nematodes. Ndeme Atibalentja, University of Illinois.
- Characterization of the *Pseudomonas* genus of bacteria for plant-parasitic nematode control. Christopher Taylor, Donald Danforth Plant Science Center.

In addition to these keynote talks, oral presentations were given by students attending the workshop. Research priorities and needs, methodology, analysis, education, and funding strategies were also addressed. A collection of manuscripts from several keynote speakers from each session has been compiled and constitutes this current issue of Symbiosis.

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Participants of the Nematode-Bacteria Symbioses Workshop.
From top to bottom (left to right): Jonathan Dworkin, Paul De Ley, Elad Chiel, Walter Tita. Second row (left to right): Louis Tisa, Oleksander Holovachov, Larry Duncan, Creg Darby, Ralf Sommer, Ming Lee, Elodie Ghedin. Third row (left to right): Todd Ciche, Ndeme Atibalentja, Joseph Coolon, Elissa Hallem, Anne Estes, Kathryn Plichta. Fourth row (left to right): Scott Peat, Katrin Daehnel, Donald Dickson, Sara Lustigman, Christopher Taylor, David Bird. Fifth row (left to right): Barry Goldman, Daniel Bumbarger, Susan Bornstein-Forst, Istvan Molnar, Steven Forst, Joanna Gress. Sixth row (left to right): Valentina Galstova, Yolanda Reyes-Vidal, Yolanda Flores-Lara, Tiara King, Irma De Ley, Patricia Stock, Heidi Goodrich-Blair, Sam-Kyu Kim.